



The occurrence and biogeographic significance of the southern Spiny pocket mouse *Heteromys australis* in Venezuela

By R. P. ANDERSON and P. J. SORIANO

Natural History Museum and Biodiversity Research Center, and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas, USA, and Departamento de Biología, Facultad de Ciencias, Universidad de los Andes, Mérida, Venezuela

Receipt of Ms. 21. 09. 1998

Acceptance of Ms. 27. 11. 1998

Key words: *Heteromys*, spiny pocket mice, biogeography, Andes, Venezuela

Although the origin and center of diversity of the rodent family Heteromyidae (spiny pocket mice and relatives) lie in North or Central America (ROGERS 1990), two species of *Heteromys* are known to inhabit northwestern South America. *Heteromys anomalus* (Thompson, 1815) is distributed across northern Venezuela and Colombia and in the Río Magdalena Valley of central Colombia. *Heteromys australis* Thomas, 1901 is known only from northwestern Ecuador north through western Colombia to eastern Panama and east through the Colombian Andes to near Bogotá (WILLIAMS et al. 1993).

We herein report a specimen of *Heteromys australis* from the Cordillera de Mérida in northwestern Venezuela, extending the distribution of this species ca. 350 km to the northeast across the Depresión del Táchira. At present, the nearest museum records of *H. australis* are from the western slopes of the Cordillera Oriental in Colombia. The specimen is an adult female (CVULA I-3503), consisting of a skin, skull, and partial post-cranial skeleton from Presa La Honda, 10 km SSE Pregonero, Estado Táchira, at 1100 m. OCHOA and SORIANO (1991) previously reported this individual as *H. anomalus* based on distribution.

To confirm the species identity, we compare this individual with Venezuelan specimens of *H. anomalus* and with *H. australis* from the eastern extent of its range in Colombia. Dental and pelage criteria for age classification of specimens follow ROGERS and SCHMIDLY (1982), as do cranial measurements (Tab. 1). The following specimens form the basis for our comparisons. Museum abbreviations follow HAFNER et al. (1997) when available: Colección de Vertebrados de la Universidad de los Andes, Mérida (CVULA), The Field Museum, Chicago (FMNH), Instituto de Ciencias Naturales, Bogotá (ICN), and Museo del Instituto La Salle, Bogotá (MLS).

Specimens Examined – *Heteromys anomalus* (64): Venezuela: Estado Barinas, Barinitas (1, CVULA I-2329), Barragán-Barinitas, 400–440 m (3, CVULA I-837, 904, 1161), Cerro Alto, 3 km N La Soledad, 1500–1580 m (13, CVULA I-846, 924, 926, 1037, 1040-2, 1044-8, 1294), Cerro Alto, 2 km NW La Soledad, 1460–1600 m (3, CVULA I-5924, 5932, 5939), El Palmar, N Barinitas, 1000 m (1, CVULA I-1049), Hacienda Las Matas, 40 km SE Barinas, 270 m (4, CVULA I-4015, 4048, 4297, 4346); Estado Lara, El Blanquito, P.N. Yacambú, 9 km SE Sanare, 1600 m (10, CVULA I-2695, 2728, 2732, 2736, 2741-3, 2750, 2754-5), El Blanquito, P.N. Yacambú, 17 km SE Sanare, 1600 m (1, CVULA I-6162); Estado Mérida, Bejuquero, W Zea, 600 m (2, CVULA I-256-7), Capazón, La Azulita, 1000 m (4, CVULA I-1038-9, 1043, 1047), Cucuchica, 6 km E Tovar, 1200–1250 m (10, CVULA I-5971, 5986-8, 5993, 6003-4, 6008-9, 6019), El Vigía, Hacienda El

Table 1. External and cranial measurements (mm) for *Heteromys* of age classes 3 and 4 (ROGERS and SCHMIDLY 1982) from selected localities in Colombia and Venezuela. See text for exact localities and specimen numbers. Means plus or minus standard errors are given, followed by sample sizes. The sample of *H. australis* from Pregonero represents the single specimen of that species known from Venezuela (CVULA I-3503).

	<i>H. australis</i> : Huila, Río Suaza (Colombia)	<i>H. australis</i> : Táchira, Pregonero (Venezuela)	<i>H. anomalous</i> : Barinas, Cerro Alto (Venezuela)
Total length	274.2 ± 7.82, 12	268	290.0 ± 8.82, 6
Tail length	149.0 ± 3.14, 12	152	160.2 ± 6.80, 6
Hind foot length	33.7 ± 0.31, 12	34	35.8 ± 0.40, 6
Ear length	17.5 ± 0.26, 12	19	19.0 ± 0.58, 6
Greatest skull length	34.6 ± 0.33, 7	32.7	35.9 ± 0.60, 2
Zygomatic breadth	16.3 ± 0.16, 8	n/a	17.2 ± 0.34, 3
Rostral length	15.1 ± 0.30, 9	13.7	15.4 ± 0.31, 3
Nasal length	13.5 ± 0.21, 9	13.0	13.8 ± 0.15, 3
Least interorbital constriction	8.3 ± 0.10, 10	7.5	8.5 ± 0.15, 6
Mastoid breadth	15.0 ± 0.08, 6	14.8	15.7 ± 0.25, 4
Maxillary toothrow length	5.2 ± 0.06, 11	5.4	5.6 ± 0.13, 6
Interparietal width	8.4 ± 0.14, 7	9.1	9.3 ± 0.15, 3
Interparietal length	4.6 ± 0.12, 6	5.4	5.0 ± 0.12, 3
Skull depth	10.9 ± 0.14, 7	10.7	11.2 ± 0.19, 4

Roble, 150 m (1, CVULA I-894), Finca Mesa Rica, Cucuchica, 8 km W Tovar, 1250 m (1, CVULA I-6024), Hacienda La Trinidad, Caño Tigre, 370 m (2, CVULA I-2528-9), La Cuchilla del Niño, 2 km SW Zea, 1250 m (1, CVULA I-6021); Estado Táchira, San Pedro del Río, 12 km W Michelena (1, CVULA I-6196), Río Potosí, Uribante, 1050 m (1, CVULA I-2516); Estado Trujillo, Macizo de Guaramacal, 6 km SE Boconó, 2430 m (1, CVULA I-2960); Estado Zulia, El Tucuco, 46 km SSW Machiques, 300–400 m (2, CVULA I-1890, 5698), Río Arajamo, Sierra de Perijá, 1000 m (2, CVULA I-1507-8). *Heteromys australis* (20): Colombia: Departamento de Boyacá, Serranía Las Quinchas, Puerto Boyacá, 1175 m (2, ICN 13150-1); Departamento de Cundinamarca, Paime (1, MLS skin #2303); Departamento del Huila, Río Suaza Río Aguas Claras, near San Adolfo, 1400 m (16, FMNH 71191–71206). Venezuela: Estado Táchira, Presa La Honda, 10 km SSE Pregonero, 1100 m (1, CVULA I-3503).

The specimen of *H. australis* from Pregonero (CVULA I-3503) is a young adult female in the process of molting into adult pelage. The permanent premolars are well worn, and the lophes of most upper molars form a u-shaped crown pattern, placing it between age classes III and IV of ROGERS and SCHMIDLY (1982). Externally, it displays the dark, slaty black dorsal pelage characteristic of *H. australis* with only the slightest grizzling of ochraceous hairs, in contrast to the usually brownish, more grizzled dorsum of *H. anomalous*. The tail is only indistinctly bicolored, with some dark hairs present on its ventral surface, as in *H. australis*, and is much shorter than those of *H. anomalous* (Tab. 1).

Cranially, the Venezuelan specimen agrees with *H. australis* in its relatively wider and absolutely shorter skull than *H. anomalous*, which have more elongated skulls. It also presents the wide, inflated braincase characteristic of *H. australis* (WILLIAMS et al. 1993). The rostrum is narrower and, although the zygomatic arches are broken, the anterior roots of the zygomatic arch are clearly more gracile than in *H. anomalous*. The masseteric fossa is only shallowly excavated in Venezuelan and Colombian specimens of *H. australis*, whereas that of *H. anomalous* is deeply excavated. These characters hold up for all within-age-class comparisons for age classes III and older.

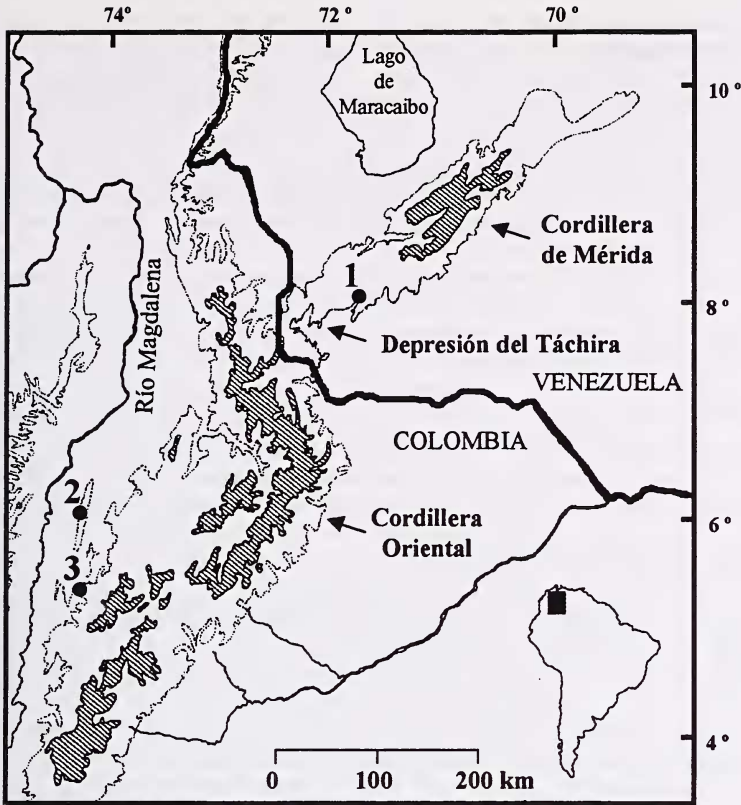


Fig. 1. Map showing the known collection localities of *Heteromys australis* in the eastern extent of its range in Venezuela and Colombia. The species continues its distribution to the west in Colombia, Ecuador, and Panama. The 1000 m contour is marked by a dotted line, and areas over 3000 m are stippled. 1) = Pregonero, Táchira; 2) = Serranía Las Quinchas, Boyacá; 3) = Paime, Cundinamarca. See text for exact localities and specimen numbers.

This range extension places *H. australis* to the east of the Depresión del Táchira, an area of low hills and ridges which separates the Cordillera de Mérida from the Cordillera Oriental of the Andes (Fig. 1) and which constitutes an important zoogeographic barrier (SORIANO et al. 1999). Whereas *H. anomalus* tolerates a wide precipitation range, *H. australis* is found only in wet lowland and montane forests. Thus, the present habitat in the Depresión del Táchira is likely too xeric for *H. australis*. We hypothesize that *H. australis* probably colonized the Pregonero area during a past glacial period and that its present-day occurrence there represents a relict population disjunct from populations in the Cordillera Oriental.

Heteromys australis is likely present at middle elevations elsewhere in the southern portion of the Cordillera de Mérida (where it occurs in close parapatry with *H. anomalus* – note CVULA I-2516), and may eventually also be found on the eastern slopes of the Cordillera Oriental. The specimen from Pregonero has a much thinner alisphenoid strut and a more constricted interorbit than Colombian specimens of the same species. Hence, this Venezuelan population of *H. australis* may be slightly differentiated from the more western populations. However, at this time, we do not recognize it as subspecifically distinct on the basis of a single specimen.

The range retraction and subsequent isolation we hypothesize for *H. australis* parallel the distributional patterns of other montane taxa in the region. CUATRECASAS (1986) illustrated probable distributions of the rosette "frailejones" of the plant genus *Espeletia* (Asteraceae), uninterrupted through the wet páramos of the northern Andes during the latter part of the Last Glacial, in contrast to the present, fragmented distribution of the genus. Similarly, LYNCH (1986) presented a phylogeny and distributional map for the monophyletic *Eleutherodactylus devillei* assembly, five species of leaf litter frogs restricted to cloud forests and subpáramo habitats in the northern Andes. In that system, *E. bricensi*, from the Mérida Andes, is the most basal member of the clade, presumably the first to undergo a vicariant separation from the ancestral populations to the southwest and undergo speciation.

Given the North or Central American origin of heteromyids, populations of *H. australis* probably only have experienced one or a few Pleistocene glacial cycles in the region, whereas these other groups have a long history in the Andes. If the range disjunction identified for *H. australis* originated with Pleistocene glacial bouts, as argued here, then such a pattern provides evidence that the species was already present in South America before the Holocene. This suggestion counters MARSHALL et al. (1982), who assumed a Recent dispersal of heteromyines into South America based on the lack of a fossil record for the group. Rather, it is compatible with ROGERS' (1990) biochemical evidence that suggested a relatively old origin of the *H. anomalus* and *H. australis* groups, long before the end of the last glaciation.

Other unexpected mammals have been collected at Pregonero as well, indicating the area's possible biogeographic importance. The aquatic rat *Neusticomys mussoi* is known only from its type locality near Pregonero (OCHOA and SORIANO 1991). In addition, the short-tailed opossum *Monodelphis adusta* was first reported for Venezuela from this locality (SORIANO 1987), but subsequently has been found near Zea on the northern-facing slopes of the Cordillera de Mérida (RAMONI-PERAZZI et al. 1994). The only known specimens of the phyllostomid bat *Sturnira tildae* in the Cordillera de Mérida also were collected in Táchira near Pregonero (OCHOA et al. 1993). The fauna of this part of the Cordillera, the Río Uribante drainage, may share greater similarity with that of the Colombian Andes than with the rest of the Cordillera de Mérida. However, the scarcity of collections from similar elevations elsewhere in the Cordillera de Mérida precludes definitive conclusions regarding general distributional patterns of these small mammals.

Acknowledgements

We thank the following curators for access to specimens under their care: ALBERTO CADENA (ICN), HERMANO ROQUE CASALLAS and ARTURO RODRÍGUEZ (MLS), and BRUCE D. PATTERSON (FMNH). The manuscript benefited greatly from careful comments offered by MICHAEL D. CARLETON, MARCELA GÓMEZ-LAVERDE, A. TOWNSEND PETERSON, DUKE S. ROGERS, NORMAN A. SLADE, and ROBERT M. TIMM. This work was partially funded by the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICIT) and the Consejo de Desarrollo Científico, Humanístico y Tecnológico de la Universidad de los Andes (CDCHT-ULA) through the grants RP-VII-240056 and C-564-92-01-A, respectively. ANDERSON'S research on *Heteromys* was supported by a National Science Foundation Graduate Fellowship, a Fulbright Fellowship (Colombia-USA), and by grants from the E. RAYMOND HALL Fund (KUNHM Mammal Division) and the THOMAS J. DEE Fund (FMNH).

References

- CUATRECASAS, J. (1986): Speciation and radiation of the Espeletiinae in the Andes. In: High altitude tropical biogeography. Ed. by F. VUILLEMIER and M. MONASTERIO. New York, Oxford: Oxford Univ. Press. Pp. 267–303.

- HAFNER, M. S.; GANNON, W. L.; SALAZAR-BRAVO, J.; ALVAREZ-CASTAÑEDA, S. T. (1997): Mammal collections in the Western Hemisphere: A survey and directory of existing collections. Lawrence, Kansas: American Soc. Mammal. and Allen Press.
- LYNCH, J. D. (1986): Origins of the high Andean herpetological fauna. In: High altitude tropical biogeography. Ed. by F. VUILLEMIER and M. MONASTERIO. New York, Oxford: Oxford Univ. Press. Pp. 478–499.
- MARSHALL, L. G.; WEBB, S. D.; SEPKOSKI, J. J. JR.; RAUP, D. M. (1982): Mammalian evolution and the great American interchange. *Science* **215**, 1351–1357.
- OCHOA, J.; SORIANO, P. J. (1991): A new species of water rat, genus *Neusticomys* Anthony, from the Andes of Venezuela. *J. Mammalogy* **72**, 97–103.
- OCHOA, J.; SORIANO, P. J.; LEW, D.; OJEDA C., M. (1993): Taxonomic and distributional notes on some bats and rodents from Venezuela. *Mammalia* **57**, 393–400.
- RAMONI-PERAZZI, P.; BIANCHI, G.; MOLINA, M. (1994): Hallazgo de la comadreja colicorta *Monodelphis adusta* (Thomas, 1897) en la cuenca del Lago de Maracaibo, Venezuela. *Acta Cient. Venez.* **45**, 325–326.
- ROGERS, D. S. (1990): Genic evolution, historical biogeography, and systematic relationships among spiny pocket mice (subfamily Heteromyinae). *J. Mammalogy* **71**, 668–685.
- ROGERS, D. S.; SCHMIDLY, D. J. (1982): Systematics of spiny pocket mice (genus *Heteromys*) of the *desmarestianus* group from Mexico and northern Central America. *J. Mammalogy* **63**, 375–386.
- SORIANO, P. J. (1987): On the presence of the short-tailed opossum *Monodelphis adusta* (Thomas) in Venezuela. *Mammalia* **51**, 321–324.
- SORIANO, P. J.; DÍAZ DE P., A.; OCHOA, J.; AGUILERA, M. (1999): Las comunidades de roedores de Los Andes de Venezuela. In: Biodiversidad en Iboamérica, Vol. 3. Ed. by G. HALFFTER. México: Centro de Ecología, UNAM and Fondo de Cultura Económica. Pp. 197–213 (in press).
- WILLIAMS, D. F.; GENOWAYS, H. H.; BRAUN, J. K. (1993): Taxonomy and Systematics. In: Biology of the Heteromyidae. Ed. by H. H. GENOWAYS and J. H. BROWN. American Soc. Mammal. Special Publ. No. **10**, 38–196.

Authors' addresses: ROBERT P. ANDERSON, Natural History Museum. University of Kansas, Lawrence, KS 66045-2454, USA and PASCUAL J. SORIANO, Departamento de Biología, Facultad de Ciencias, Universidad de los Andes, Mérida 5101, Venezuela.